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Notes on *Peromyscus* (Muridae) of Mexico and Central America

BY GUY G. MUSSER¹

In the most recent classification of *Peromyscus* (Hooper and Musser, 1964) the allocation of several species to species-groups was questioned and considered tentative. Subsequently, Emmet T. Hooper and I examined representatives of the questionable forms along with samples of species described and named after the classification was published. Hooper (in press) has summarized the results of those examinations in a new treatment of the classification of *Peromyscus*. He suggested that I pursue the study and try to answer some questions that were raised during our various studies on *Peromyscus*.

In the present paper I have attempted to clarify the status of a few species of Middle American *Peromyscus*. I also discuss misidentified series reported in the literature, known geographic ranges of those species, and new data on taxonomy and habitat. Some of the specimens and information recorded here were obtained in Mexico in 1963, 1964, and 1965 in the course of collecting data for a systematic review of Mexican *Sciurus* (Musser, 1968).

I am grateful to curators of collections in the American Museum of Natural History (A.M.N.H.), the University of Kansas Museum of Natural History (K.U.), University of California Museum of Vertebrate Zoology (M.V.Z.), University of Michigan Museum of Zoology

¹ Archbold Assistant Curator, Department of Mammalogy, the American Museum of Natural History.

(U.M.M.Z.), and the United States National Museum of the Smithsonian Institution (U.S.N.M.) for allowing me to study specimens in their care. Mr. George G. Goodwin of the American Museum graciously turned over to me all Oaxacan specimens of *Peromyscus* that were pertinent to my studies. Our discussions of the classification of *Peromyscus* in general, and the correct allocation of Oaxacan forms in particular, have been enjoyable, although we disagree on many points. In his manuscript on Oaxacan mammals (Goodwin, in press) some of his taxonomic conclusions regarding certain species of *Peromyscus* probably differ from those presented here. Permits to collect specimens in Mexico are from the Secretaría de Agricultura y Ganadería de México and were kindly supplied by Dr. Rodolfo Hernández Corzo, Director General of the Departamento de Conservación de la Fauna Silvestre. Dr. Emmet T. Hooper, of the University of Michigan Museum of Zoology, has carefully read the manuscript; I appreciate his good suggestions.

Data were obtained from dry study skins with skulls, and specimens preserved in fluid. Total length, length of tail vertebrae, length of hind foot, and length of ear (from notch) are those of the collectors and were taken from skin labels. Length of head and body was computed as total length minus length of tail. Cranial measurements were taken either with dial calipers graduated in tenths of millimeters, or by the craniometer described by Anderson (1968) with the Spaulding instrument attached. The limits of those measurements are the same as described for *Peromyscus truei* by Hoffmeister (1951, p. 28) with the exception of the length of the rostrum. This was measured from the tip of the nasals to the posterior margin of the infraorbital notch and parallel to the long axis of the skull.

THE *ANGELENSIS-MEXICANUS* PROBLEM

The populations of *Peromyscus* from the Pacific slopes of Oaxaca that Osgood (1904, p. 69) described as *angelensis* were considered to be most closely allied to *P. banderanus* and were regarded as a subspecies of that species. Later, however (1909, p. 210), Osgood pointed out the morphological divergence of *angelensis* from *banderanus* (including *P. b. vicinor* Osgood, 1904, p. 68) and its similarities with samples of *P. mexicanus*. During our various studies of *Peromyscus*, Hooper and I have suspected that *angelensis* may be a geographic form of *mexicanus* rather than of *banderanus*, and these suspicions have recently been recorded elsewhere (Hooper, in press).

I have now had the opportunity to examine the material in the United States National Museum that Osgood allocated to *angelensis* (including the holotype), examples in the University of Michigan Museum of Zoology, and specimens in the American Museum of Natural History that are referable to that taxon (Goodwin, 1955, 1956). I was also able to examine series of all named forms of *banderanus* and *mexicanus* from the entire known geographic range of each of the species. The results of my study indicate that *angelensis* belongs in the species *P. mexicanus* and is not a geographic form of *P. banderanus*, and that both species occur sympatrically in Guerrero.

The following 113 specimens from Guerrero and Oaxaca are referable to *angelensis*; they are listed geographically from west to east:

GUERRERO: Near Ometepe, 200 feet, one (U.S.N.M.).

OAXACA: Pinotepa Nacional, one (U.S.N.M.); Pinotepa de Don Luís, two (A.M.N.H.); Boquilla de Río Verde, one (A.M.N.H.); Santos Reyes Nopala, 3000 feet, three (A.M.N.H.); 2 miles east of San Gabriel Mixtepec, 10 (A.M.N.H.); mainland near Escondido Bay, three (U.M.M.Z.); Puerto Angel, 20 (U.S.N.M.); Pluma Hidalgo, two (U.S.N.M.); San Felipe Lachilló, one (A.M.N.H.); Zazamora, 15 miles west of Tequisistlán, 3000 feet, seven (A.M.N.H.); Tenango, about 25 miles west of Tehuantepec, 5000 feet, four (A.M.N.H.); Cerro Otate, 5000 feet, two (A.M.N.H.); La Concepción, 7 miles northeast of Tenango, 4000 feet, one (A.M.N.H.); Cerro Arenal, 19 miles west of Tehuantepec, 3500 feet, six (A.M.N.H.); Santa Lucía, 17 miles west of Tehuantepec, 4000 feet, 41 (A.M.N.H.); Cerro Tres Cruces, 8 miles east of Tenango, 4000 feet, five (A.M.N.H.); Arroyo San Juan, 15 miles west of Tehuantepec, three (A.M.N.H.).

Specimens listed above were compared with the following examples of *P. banderanus* (typical *banderanus* and *vicinor*):

NAYARIT: El Valle de Banderas, one (A.M.N.H.).

JALISCO: Navarrete, one (U.S.N.M.).

COLIMA: Manzanillo, five (U.S.N.M.); near Colima, seven (U.S.N.M.); Hacienda San Antonio, one (U.S.N.M.); Hacienda Magdalena (Pueblo Juárez), 12 (three A.M.N.H.; nine U.S.N.M.).

MICHOACÁN: Los Reyes, two (U.S.N.M.); La Salada, five (U.S.N.M.); La Huacana, four (U.S.N.M.).

GUERRERO: Acahuitzotla, three (U.S.N.M.); Acapulco, nine (U.S.N.M.); El Limón, two (U.S.N.M.); near Ometepe, four (U.S.N.M.).

Osgood (1909) adequately described both typical *banderanus* and *angelensis* and provided measurements of each. He pointed out that, although *angelensis* is somewhat larger than *banderanus*, both forms resemble each other closely in color and texture of pelage. With those features, however, close resemblance ends and, the two kinds are clearly distinguishable in other external features, cranial characters, and genitalia, as follows.

TAIL: The tail in *banderanus* is slightly more hairy than in *angelensis*. The dorsal surface tends to be brownish, unlike the darker blackish tail of *angelensis*. In *banderanus* the under surface of the tail is lighter than above and usually monocolored, but may be slightly splotched with brownish and yellowish hues. In *angelensis*, however, the tail tends to be more yellowish below and is usually conspicuously and irregularly blotched with brownish hues, as is that of typical *P. mexicanus*. These distinctions between the two kinds are average, not absolute.

HIND FOOT: In all specimens of *banderanus* the soles of the hind feet are naked from the tips of the toes to the calcaneum as Osgood described them. A few minute hairs are scattered over the sole, generally near the heel, on some specimens. The absence of hair from the sole is evident on all age groups seen, from juveniles to old adults.

In all specimens referable to *angelensis*, however, the sole of the hind foot is naked only from the tips of the toes posterior to the level of the last plantar tubercle. There are invariably a few scattered short hairs in this area. The remainder of the sole to the calcaneum is covered by hair that varies from long and dense, forming whorls over the heel, to short and sparse, approaching, but never reaching, the condition seen in *banderanus*. Differences in the density of hairs over the heel can be seen with the unaided eye, but are best seen under $6\times$ – $12\times$ magnification. On this single character all specimens of *angelensis* can be separated from those of *banderanus*. The condition in *angelensis* is like that in populations of *P. mexicanus* and in most other species of *Peromyscus*.

SKULL: The skull of *P. banderanus* is distinguishable at once from that of *angelensis* by its conspicuous supraorbital shelves bounded by ridges that extend well beyond the frontoparietal suture and onto the sides of the braincase (fig. 1), by its larger and distinctively shaped interparietal, and by its more elongate and shallower braincase. Other cranial differences between *banderanus* and *angelensis* were listed by Osgood (1909, p. 210). Features of the skull seen in *angelensis* are common to those of *P. mexicanus*, not to those of *banderanus*. The supraorbital shelf is slightly better developed and more frequent in samples of *angelensis* than in many other sampled populations of *mexicanus*, but it is equaled by the size of the shelves seen in samples of such forms as *P. m. putlaensis* and particular samples of *P. m. mexicanus*, *P. m. totontepecus*, and *P. m. saxatilis*.

TEETH: The teeth of *angelensis* are slightly larger, and their topography is less complex, than those of *banderanus*. The relatively simple topography of the teeth in *angelensis* is like that described and illustrated for *P. mexicanus* by Hooper (1957, pp. 36–37). In contrast, the accessory dental structures of *banderanus* are better developed than those of *angelensis*. In



FIG. 1. Dorsal and ventral cranial views of *Peromyscus banderanus* and *P. mexicanus*. Left: *P. b. banderanus*, U.S.N.M. No. 45336, from Hacienda Magdalena (Pueblo Juárez), Colima. Right: *P. m. angelensis*, A.M.N.H. No. 190335, from 2 miles east of San Gabriel Mixtepec, Oaxaca. Photographed by Robert E. Logan. $\times 2$.

the first and second upper and lower molars the mesolophids and mesolophids are joined to the respective mesostyles and mesostylids forming conspicuous but low accessory ridges in each tooth. The ectostylids of the first two lower molars are prominent and often joined to a low ectolophid. In total dental complexity, *banderanus* would fit between *mexicanus* and *yucatanicus* (Hooper, 1957), for example.

GENITALIA: I was able to examine the glans penis of six specimens of *angelensis*. One example (A.M.N.H. No. 190340), from 2 miles east of San Gabriel Mixtepec, is preserved in fluid. The glans penis of the other specimens was taken from dry study skins, refurbished, and processed as described by Hooper (1958). The five examples are: an adult from Bocadillo Río Verde (A.M.N.H. No. 207438); a young adult from Cerro Arenal (A.M.N.H. No. 145314); and three specimens from Santa Lucía, two subadults (A.M.N.H. Nos. 143313 and 143337) and a young adult (A.M.N.H. No. 143385). In all six specimens the glans penis is long and slender, with two dorsal lappets, one ventral lappet that forms the rim of the meatus urinarius, and an elongate protactile tip; the baculum is a long slender rod with a small base. The structure and size are typical of the glans of *P. mexicanus* (Hooper, 1958, p. 14, pl. 5), and unlike the tiny and simple awl-shaped glans that is distinctive of *banderanus* (1958, p. 18, pl. 10).

SYMPATRY: Evidence for sympatry between *banderanus* and *angelensis* comes from five specimens (in the United States National Museum) collected by E. W. Nelson and E. A. Goldman near Ometepec, southeastern Guerrero, on February 13 and 14, 1895. Goldman (1951, p. 156) indicated that specimens labeled "Near Ometepec" were obtained approximately 9 miles southeast of Ometepec at 200 feet in elevation on the bank of the Río Santa Catarina, a tributary of the Río Ometepec. In characteristics of size, tail, hind feet, skull, and teeth, four specimens (U.S.N.M. Nos. 71420-71423) are *banderanus*; their features match those in samples of typical *banderanus* from elsewhere in Guerrero. Features of the fifth specimen, an adult female (U.S.N.M. No. 71424), fall within the range of variation seen in series of *angelensis* from Puerto Angel, Oaxaca. This specimen, like the others allocated to *angelensis*, is an example of *P. mexicanus*. This specimen of *angelensis* and two of *banderanus* were taken on the same day, February 14. Unfortunately, there are no other data by which the precise ecological relationships of the two species in southeastern Guerrero can be determined.

Until *Peromyscus mexicanus* is revised taxonomically, *angelensis* should be tentatively arranged as a subspecies of *P. mexicanus*. Populations of *angelensis* occupy the coastal plain and adjoining uplands of southeastern

Guerrero eastward through southern Oaxaca to the southwestern foothills of the Sierra de Miahuatlán near the Isthmus of Tehuantepec. Judged from material at hand from the Tehuantepec region, *angelensis* and *mexicanus* intergrade morphologically on the Pacific side of the isthmus.

Peromyscus banderanus, a species of the coastal plain and interior valleys of western Mexico, is known from Nayarit southeastward to Guerrero (as outlined in the distribution map for *P. b. banderanus* and *P. b. vicinor* by Hall and Kelson, 1959, p. 653) and is sympatric with *P. m. angelensis* in southeastern Guerrero.

Two other names have been associated with *P. banderanus* in the literature: *coatlanensis* (Goodwin, 1956, p. 7) and *sloeops* (Goodwin, 1955, p. 2). I have examined the holotypes and respective paratypes upon which those names are based. Both series are examples of *P. mexicanus*, not *banderanus*, as Hooper (in press) indicated. Whether the two series represent distinctive geographic forms of *mexicanus* or fit with existing named populations must be resolved by a taxonomic revision of *mexicanus*.

SPECIMENS OF *PEROMYSCUS* FROM GUATEMALA AND HONDURAS IN THE AMERICAN MUSEUM OF NATURAL HISTORY

I have studied, in the American Museum of Natural History and the University of Michigan Museum of Zoology, specimens of *Peromyscus* from Guatemala and Honduras that were reported by Goodwin (1934 and 1942, respectively) under various names: (from Guatemala) *P. boylei levipes*, *P. guatemalensis guatemalensis* and *P. g. tropicalis*, *P. mexicanus saxatilis* and *P. m. gymnotis*, and *P. grandis*; (from Honduras) *P. boylei sacarensis*, *P. guatemalensis tropicalis*, *P. mexicanus saxatilis*, *P. stirtoni*, and *P. hondurensis*.

Some of those series warrant additional comment. They are discussed below under the names used by Goodwin.

Peromyscus mexicanus saxatilis

This form was recorded from four localities in Guatemala: Chanquejelve, Tecpám, La Primavera, and Finca Concepción (Goodwin, 1934, p. 43). The seven specimens from Chanquejelve are examples of *P. mexicanus* and are referable to *saxatilis*. Series from Tecpám, La Primavera, and Finca Concepción, however, are not examples of *mexicanus*. In characteristics of skin and skull they answer Osgood's (1909, p. 158) description of *P. oaxacensis*, and their features also match those seen in

series of *oaxacensis* from Oaxaca and Chiapas. In the Chiapas-Guatemala region some populations of *mexicanus* are superficially similar to *oaxacensis*, particularly in pelage features, but as Osgood (1909, p. 159) and Hooper (1947, p. 51) noted, the two species are always distinguishable by other external and cranial characters. *Peromyscus oaxacensis* was taken with *P. grandis* at Finca Concepción and with *P. boylei* at Tecpám and La Primavera. *Peromyscus boylei* was also trapped with *P. mexicanus* at Chanquejelve.

Goodwin (1942, p. 162) listed *P. m. saxatilis* from eight localities in Honduras: Cerro Pucca, Monte Linderos, Pucca, Muya, El Durrumbo, Sabana Grande, Cantoral, and El Colerio. All these specimens identified as *saxatilis* are representatives of *P. oaxacensis*; none is *P. mexicanus*.

Peromyscus hondurensis

This form was described from two small series (Goodwin, 1941), the holotype and two paratypes from Muya (A.M.N.H. Nos. 126742, 126743, and 126707), and six specimens from Cerro Pucca (A.M.N.H. Nos. 129959, 129963, 129964, 129967, 129968, and 130015). Ages in both series range from juveniles to young adults; older specimens are not represented. Actually, these two series are examples of *P. oaxacensis* as Hooper (in press) indicated. The type and two paratypes from Muya belong with the three specimens of *oaxacensis* from there that Goodwin thought were examples of *P. mexicanus*. Two of those three specimens originally referred to *mexicanus* are old adults; the third is younger. Similarly, the six specimens of *hondurensis* from Cerro Pucca fit with the series of 12 individuals that Goodwin had referred to *mexicanus*. The variation in age in the series of 12 also ranges from juvenile to old adult, and the younger specimens are morphologically inseparable from those of comparable age in the series of six specimens originally called *hondurensis*; both series represent the same species, *oaxacensis*. The magnitude of variation in features of the skin and skull and in the dimensions of the 18 specimens from Cerro Pucca parallels that seen in a large series of *oaxacensis* from Chiapas (35 specimens from Pueblo Nuevo Solistahuacán) in the American Museum of Natural History.

Judged from these records, the geographic range of *P. oaxacensis* penetrates farther into Central America than was thought earlier (for example, see the range map in Hall and Kelson, 1959, p. 638). The species is a forest mouse that occurs in the cool and humid highlands, and is now known from the mountains of Oaxaca (Osgood, 1909; Hooper, 1961), Chiapas (Osgood, 1909; Hooper, 1947; Villa R., 1949), southern

Guatemala, El Salvador (Burt and Stirton, 1961), and western Honduras.

Peromyscus guatemalensis tropicalis

Goodwin (1942, p. 162) listed this form from 20 localities, ranging from approximately 1000 feet to 6500 feet in elevation, in western Honduras. Although there is some variation in the tone, thickness, and length of pelage, and in the size of the body, skull, and teeth from place to place, all the series (at least those in the American Museum of Natural History and the University of Michigan Museum of Zoology) represent one species. The entire lot is best referred to *P. mexicanus* rather than to *P. guatemalensis*. In features of skin and skull the specimens from Honduras differ from typical *guatemalensis* in the same ways that other forms of *mexicanus* differ from that species (Osgood, 1909, p. 194). Like *mexicanus*, the examples from Honduras are smaller than *guatemalensis*, the under surface of their tails is usually conspicuously and irregularly mottled with yellowish and brownish hues instead of being monocolored or only slightly mottled, and the skull and teeth are much smaller and less robust than those of *guatemalensis*. For the present, the series from Honduras should be allocated to *P. m. saxatilis*. Although darker than typical *saxatilis* from northern Chiapas and northwestern Guatemala, the magnitude of variation in features of skin and skull in the lot from Honduras is similar to that seen in samples of dark *mexicanus* from Nicaragua, El Salvador, and southeastern Chiapas that have been referred to *saxatilis* by Osgood (1909, p. 203), Burt and Stirton (1961, p. 57), and Hooper (1947, p. 52). *Peromyscus oaxacensis* occurs with *P. m. saxatilis* in Honduras at El Colerio, Monte Linderos, Muya, Pucca, and Cerro Pucca, and is sympatric with *saxatilis* in parts of Chiapas and El Salvador.

Goodwin observed that the specimens from Honduras closely resemble *P. nudipes* of Costa Rica and Panama in external characteristics, an observation that also applies to most populations that are called *P. m. saxatilis* in the current literature. At present there is no accurate estimate of the biological relationships between *saxatilis* and *nudipes*. Whether *nudipes* connects with *mexicanus* through populations now called *saxatilis*, or whether it is more closely allied to *P. guatemalensis*, as Osgood (1909, p. 194) suggested, can be determined only by a thorough systematic study of the entire *mexicanus* species-group.

The name *P. guatemalensis tropicalis* is based on 23 specimens from Chimoxan (1500 feet in elevation), Guatemala (Goodwin, 1932, p. 3). I have compared that sample with 94 specimens of typical *P. guatemal-*

ensis from southern and northwestern Guatemala (Volcán San Lucas, San Lucas, and San Mateo), and with series of *P. m. saxatilis* from Guatemala (seven specimens from Chanquejelve) and Chiapas (18 examples from west of Bochil), and with large series of other races of *P. mexicanus* from elsewhere in Mexico and from Honduras and Nicaragua. Characters that distinguish *tropicalis* from typical *guatemalensis* (Goodwin, 1932, pp. 3-4) are essentially those features that separate the dark and large-bodied geographic forms of *mexicanus* from *guatemalensis* (those, for example, that distinguish *saxatilis* or *totontepecus* from *guatemalensis*). In addition, populations of *guatemalensis* occur in cool and moist forests above 6000 feet and are usually found at much higher elevations both in Chiapas and Guatemala. On the other hand, the Guatemalan sample of *tropicalis* was obtained from lowland tropical forest, a habitat more typical of *mexicanus*. My intention is not to revise the Guatemalan forms of the *mexicanus* group of species in this paper, but to point out that in morphology and habitat, *tropicalis* is of *mexicanus* type rather than of *guatemalensis* type. Any taxonomic revision of the *mexicanus* group must document carefully whether *tropicalis* actually belongs in *mexicanus* rather than in *guatemalensis*.

SUBGENUS *HABROMYS*

Osgood (1909) first pointed out the morphological and ecological similarities between *P. lepturus*, *P. lophurus*, and *P. simulatus*, and the three species have recently been grouped as a subgenus within *Peromyscus* (Hooper and Musser, 1964). All three are forest mice inhabiting cool and humid highlands of Mexico, Guatemala, and El Salvador. Their ecological tolerances are apparently narrow, and their insular geographic distributions suggest that they are relict species. Although *P. lepturus* is locally abundant, *lophurus* and *simulatus* may be rare or uncommon even in suitable habitat if present samples are any indication of their abundance. Knowledge of their biology is meager. Hooper's (1947, 1958, and 1961) distributional records and studies on the genitalia of *lepturus* and *lophurus* are notable exceptions, which have increased knowledge of the groups since Osgood's monograph. The notes that follow supplement the accounts listed above by providing additional data and interpretations of the taxonomy, habitat, and geographic distribution of *lepturus*, *lophurus*, and *simulatus*.

Peromyscus lepturus

The known geographic range of this species covers two of the north-

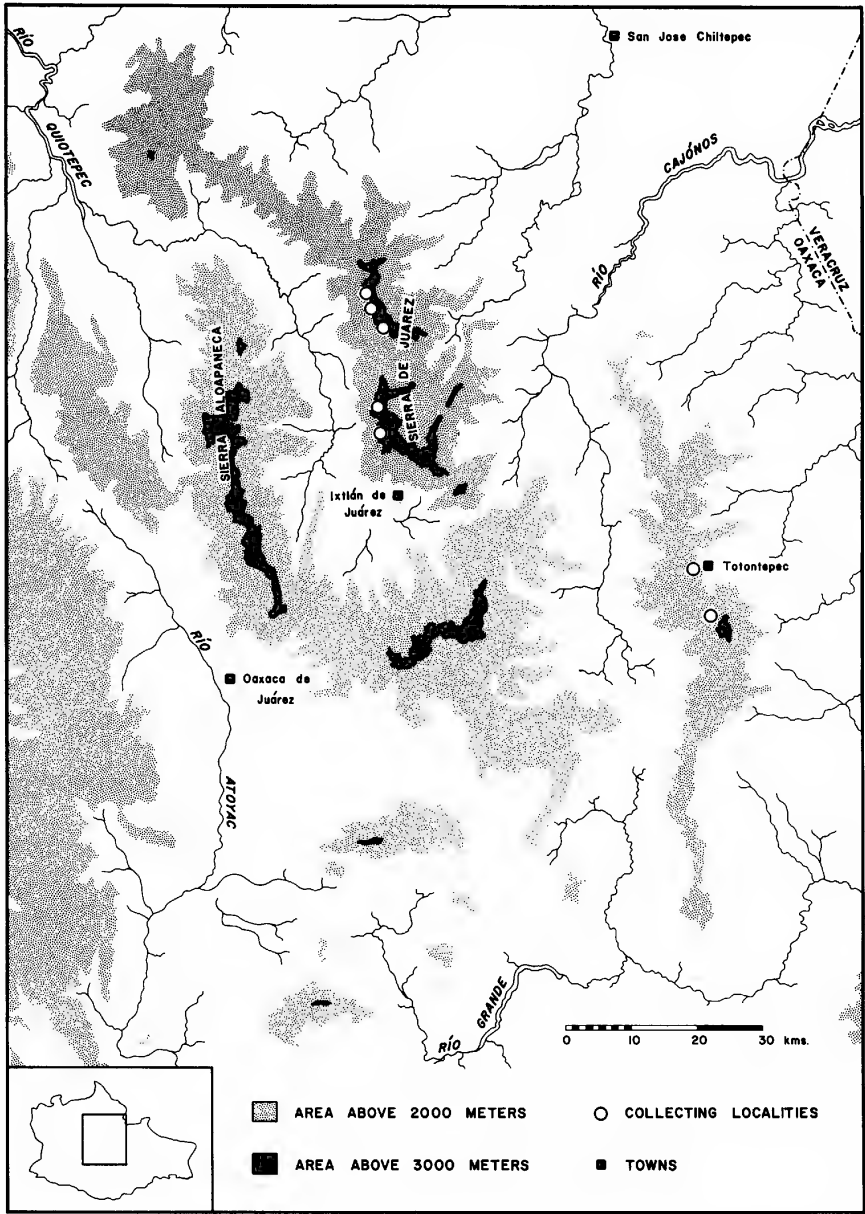


FIG. 2. The distribution of *Peromyscus lepturus* in the highlands of northern Oaxaca, as determined from specimens examined.

ward-projecting, high mountain ridges that form part of the Sierra Madre del Sur of northern Oaxaca (fig. 2). One ridge, the Sierra de Juárez, lies north and east of Cerro San Felipe. The other ridge parallels the Sierra de Juárez. Its southern high point is Cerro Zempoaltepec (Zempoalteptl on some maps and in local usage); its northern margins are at Cerro Piedra and Cerro Gavilán. This ridge is separated from the Sierra de Juárez by the valley of the Río Cajónos.

I examined specimens from the following localities (listed from north to south). *Sierra de Juárez*: slopes of Cerro Machín, about 5 kilometers northeast of Macuiltianguis, 9000 feet, nine (A.M.N.H.); south slope of Cerro Pelon, 13 road miles northeast of Llano de las Flores, 8900 feet, 41 (U.M.M.Z.); 11 road miles northeast of Llano de las Flores, 9100 feet, six (U.M.M.Z.); vicinity of Llano de las Flores, about 12 airline miles north of Ixtlán de Juárez, 9500 feet, 34 (one A.M.N.H.; 33 U.M.M.Z.); 4 road miles southwest of Llano de las Flores, 8700 feet, one (U.M.M.Z.). *Zempoaltepec Region*: Totontepec, one (U.S.N.M.); Cerro Zempoaltepec, 8200 feet, seven (one A.M.N.H.; six U.S.N.M.).

The habitat of *P. lepturus* is cold, wet cloud forest of oak, pine, and fir. In those forests the trees are draped with bromeliads, moss, lichens, and other epiphytes. A ground cover of lush herbaceous plants and shrubs is usual, and thick moss covers rotting logs, rock outcrops, and exposed parts of the forest floor. This habitat is typical in parts of the Llano de las Flores (Hooper, 1961, p. 121), the south slopes of Cerro Pelon (Musser, 1964, pp. 4 and 8), and Cerro Zempoaltepec, and near Totontepec (Goldman, 1951, pp. 210 and 228).

My trapping records indicate that *lepturus* occurs with three other species of *Peromyscus* at Cerro Pelon: *P. thomasi cryophilus*, *P. boylei levipes*, and *P. oaxacensis*. Among these *P. lepturus* is the common mouse, *thomasi* is the next most abundant, and *boylei* and *oaxacensis* are uncommon. Around Llano de las Flores, however, *lepturus* occurs only with *boylei* and *oaxacensis*. There, *lepturus* is common in the deep, cool, and wet parts of the forest, but *boylei* and *oaxacensis* are uncommon in that habitat and more abundant in the drier parts of the forest (Hooper, 1961, p. 121). *Peromyscus lepturus* has not been taken with *P. melanocarpus*, another deep-forest species, on the Sierra de Juárez, but the two species apparently occur together on Cerro Zempoaltepec (Osgood, 1909, p. 191).

Morphologically and geographically, the available samples are divisible into two lots. Samples from Cerro Zempoaltepec and Totontepec constitute one group; those from the Sierra de Juárez, the other. The series from Zempoaltepec is the basis for the name *lepturus* (Merriam, 1898, p. 118); that series and the specimen from Totontepec represent

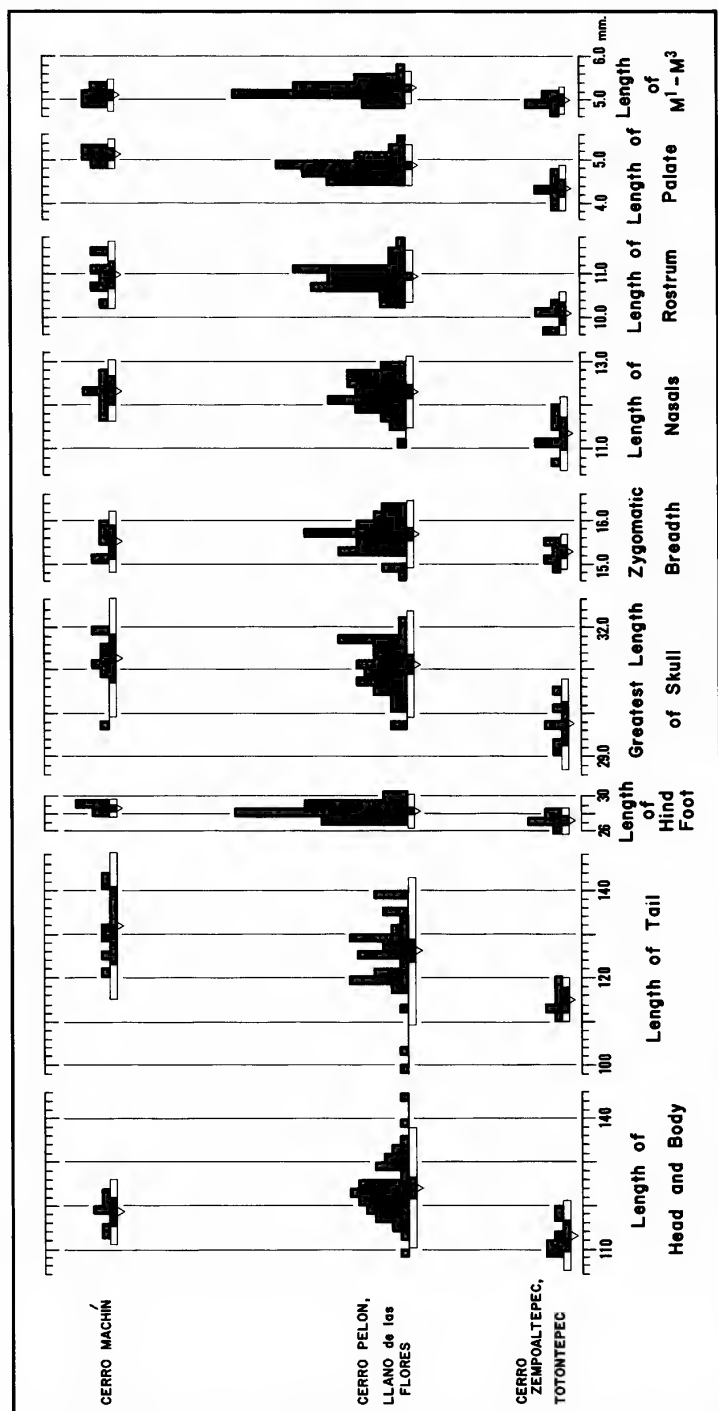


FIG. 3. Variation of external and cranial features in samples of *Peromyscus lepturus*. In each sample the mean is marked by an inverted triangle; two standard deviations on each side of the mean are shown by hollow rectangles; and the 95 per cent confidence limits of the mean are indicated by black rectangles. Each square equals one specimen. The size of each sample is indicated in table 1.

TABLE 1
MEASUREMENTS (IN MILLIMETERS) FROM SAMPLES OF ADULTS OF *Peromyscus lepturus*
(The mean and standard deviation, 95 per cent confidence limits of the mean, extremes [in parentheses],
and size of sample are listed, in that order, for each character.)

	Cerro Machín	P_t^a	Cerro Pelón, Llano de las Flores	P_g^b	Cerro Zempoaltepec, Totontepec
Length of head and body	118.7±3.6 114.9-122.5 (113-123) 6	.05-0.1	124.4±6.8 122.3-126.4 (110-145) 45	<.001	113.1±4.0 109.5-116.8 (109-119) 7
Length of tail	132.0±8.3 123.2-140.8 (122-143) 6	0.1-0.2	126.0±8.4 123.4-128.6 (100-140) 43	.001-.01	115.2±2.6 112.4-117.9 (112-119) 6
Length of hind foot	28.7±0.5 28.1-29.2 (28-29) 6	0.1-0.2	28.2±0.9 27.9-28.4 (27-30) 45	.001-.01	27.1±0.7 26.5-27.8 (26-28) 7
Length of ear ^c	— — — —	—	21.0±0.8 20.8-21.3 (20-23) 45	—	— — — —

TABLE 1—(Continued)

	Cerro Machín	P_1	Cerro Pelon, Llano de las Flores	P_2	Cerro Zempoaltepec, Totontepec
Greatest length of skull	31.23±0.68 30.66–31.79 (29.8–31.9) 8	0.5–0.6	31.08±0.58 30.90–31.25 (29.7–32.1) 45	<.001	29.77±0.53 29.21–30.32 (29.1–30.6) 6
Length of nasals	12.28±0.34 11.99–12.56 (11.7–12.8) 8	>0.9	12.29±0.43 12.16–12.42 (11.1–13.0) 44	<.001	11.36±0.43 10.96–11.75 (10.8–12.0) 7
Length of rostrum	10.99±0.39 10.66–11.31 (10.4–11.5) 8	0.6–0.7	10.94±0.30 10.85–11.03 (10.4–11.7) 44	<.001	10.08±0.24 9.83–10.34 (9.8–10.4) 6
Zygomatic breadth	15.52±0.36 15.08–15.96 (15.1–15.9) 5	0.3–0.4	15.68±0.38 15.57–15.80 (14.8–16.4) 43	.01–.02	15.28±0.19 15.08–15.49 (15.0–15.5) 6
Interorbital breadth ^c	4.65±0.14 4.53–4.77 (4.5–4.9) 8	0.5–0.6	4.62±0.14 4.58–4.66 (4.3–4.9) 45	.01–.02	4.47±0.05 4.43–4.52 (4.4–4.5) 7
Cranial breadth ^c	12.74±0.3 12.46–13.01 (12.4–13.3) 8	0.6–0.7	12.79±0.24 12.71–12.86 (12.4–13.3) 43	.02–.05	12.54±0.15 12.35–12.73 (12.3–12.7) 5

TABLE 1—(Continued)

	Cerro Machín	P_1	Cerro Pelon, Llano de las Flores	P_2	Cerro Zempoaltepec, Totontepec
Length of incisive foramina ^c	6.38±0.24 6.17-6.58 (6.0-6.6) 8	.05-0.1	6.54±0.23 6.47-6.61 (6.1-7.1) 44	.02-.05	6.34±0.26 6.10-6.58 (6.0-6.8) 7
Length of bony palate	5.15±0.17 5.01-5.29 (4.9-5.4) 8	.001-.01	4.86±0.24 4.79-4.93 (4.5-5.5) 45	<.001	4.36±0.22 4.15-4.56 (4.0-4.7) 7
Alveolar length of M ¹ -M ³	5.13±0.18 4.97-5.28 (4.9-5.4) 8	.05-0.1	5.24±0.18 5.19-5.30 (4.9-5.7) 45	<.001	4.99±0.18 4.82-5.15 (4.7-5.2) 7

^a P_1 , probability that the means of Cerro Machín and Cerro Pelon represent the same population.^b P_2 , probability that the means of Cerro Pelon and Cerro Zempoaltepec represent the same population.^c Not shown in figure 3.

the same interbreeding population. The sample from Cerro Machín in the Sierra de Juárez is the basis for the name *ixtlani* (Goodwin, 1964, p. 2). In morphology and habitat that sample is indistinguishable from series obtained near Llano de las Flores and Cerro Pelon. Size (fig. 3, table 1) and some pelage features are the principal differences between the two groups. Mice from the Sierra de Juárez have a longer head and body, longer tail, and longer feet than those from Cerro Zempoaltepec and Totontepec. The tail is more distinctly bicolored and the feet are less dusky in the Sierra de Juárez lot than in samples from Cerro Zempoaltepec, as Goodwin (1964, p. 2) noted.

Cranially, the two groups are distinguishable mainly by size (see figs. 1 and 2 in Goodwin, 1964, pp. 2-3). Specimens from the Sierra de Juárez are significantly larger than those from Cerro Zempoaltepec and Totontepec in the nine cranial measurements I tested. The greatest difference in size is seen in the length of the rostrum. This feature distinguishes 83 per cent of the Zempoaltepec series from 94 per cent of the sample from Sierra de Juárez. The position of the incisive foramina, relative to a plane across the anterior border of the first molars, which Goodwin (1964, p. 3) used to help distinguish the Cerro Machín series from the Zempoaltepec sample, does not hold up in the large series from Cerro Pelon and Llano de las Flores.

Goodwin (1964) regarded *ixtlani* as specifically distinct from *lepturus*—an estimate based on fewer specimens than are available to me. The material I have examined, however, clearly represents a single species comprised of two insular groups. These are ecologically similar, but morphologically distinctive, and intergrade through individual variation. Present knowledge of variation within *lepturus* is best shown by placing the samples from Cerro Zempoaltepec and Totontepec in *P. l. lepturus*, and using the combination, *P. l. ixtlani*, for mice of the Sierra de Juárez (Llano de las Flores, Cerro Pelon, and Cerro Machín).

If the variation seen in present samples is a reliable estimate of variation in each population of *lepturus*, then the degree of morphological difference between the two sets of samples suggests that the population on the Sierra de Juárez is isolated from that in the Zempoaltepec region, and there is incomplete gene flow between them at the present time. Certainly the two populations are physically isolated by the long, deep valley of the Río Cajónos. If the two populations are contiguous at all, the place would be to the south along the main backbone of the Sierra Madre north and northeast of the Valley of Oaxaca de Juárez. The few collections of mammals from this area, mainly from Cerro San Felipe (the southern high point of the Sierra Aloapaneca), however,

TABLE 2

MEASUREMENTS (IN MILLIMETERS) FROM SAMPLES OF *Peromyscus lophurus* AND *Peromyscus simulatus*
(The mean and standard deviation, extremes, and size of sample are listed for each character.)

	<i>P. lophurus</i>										<i>P. simulatus</i>	
	San Cristóbal, Chiapas	Pinabete, Chiapas	Triunfo, Chiapas	Todos Santos, Guatemala	Cajal, Guatemala	Volcán Tajumulco, Guatemala	U.M.M.Z. No. 99579	Los Esesmilés, El Salvador	M.V.Z. No. 131812*			
Length of head and body	98.0±5.3 91-103 4	100.5±8.1 89-108 4	101.2±4.3 96-106 5	103.3±4.2 99-109 4	107.5±0.7 107-108 2	107	105	105	81.0±1.4 80-82 2			
Length of tail	105.5±2.9 103-108 4	108.0±5.1 101-113 4	112.4±2.9 108-115 5	105.5±4.0 102-111 4	114.0±9.9 107-121 2	106	115	115	82.5±6.4 78-87 2			
Length of hind foot	23.5±0.6 23-24 4	24.7±0.5 24-25 4	21.0±1.0 20-22 5	24.5±0.6 24-25 4	24.5±0.7 24-25 2	25	24	24	22.0±1.4 21-23 2			
Length of ear	— — —	— — —	16.4±1.5 14-18 5	— — —	— — —	21	16	16	— — —			
Greatest length of skull	26.75±0.70 26.4-27.8 4	27.40±0.74 26.5-28.1 4	26.88±0.77 26.3-28.0 4	27.48±0.46 27.0-28.1 4	28.40±0.28 28.2-28.6 2	27.1	26.8	26.8	25.3±1.41 24.3-26.3 2			
Length of nasals	9.93±0.13 9.8-10.1 4	10.10±0.22 9.9-10.4 4	9.78±0.49 9.3-10.3 5	10.28±0.17 10.1-10.5 4	10.60±0.42 10.3-10.9 2	10.2	10.0	10.0	9.50±0.42 9.2-9.8 2			

TABLE 2—(Continued)

	<i>P. lophurus</i>					<i>P. simulatus</i>				
	San Cristóbal, Chiapas	Pinabete, Chiapas	Triunfo, Chiapas	Todos Santos, Guatemala	Calel, Guatemala	Volcán Tajumulco, Guatemala	U.M.M.Z. No. 99579	Los Esmeriles, El Salvador	M.V.Z. No. 131812	Cofre de Perote, Veracruz
Length of rostrum	8.68±0.40 8.2-9.1 4	8.88±0.13 8.7-9.0 4	8.76±0.29 8.5-9.2 5	9.07±0.21 8.9-9.3 3	9.40±0.28 9.2-9.6 2	8.7	8.8	8.6	—	—
Zygomatic breadth	13.67±0.31 13.4-14.0 3	14.13±0.66 1.33-14.9 4	13.83±0.21 13.6-14.0 4	14.38±0.15 14.3-14.6 4	14.60±0.71 14.1-15.1 2	13.9	14.6	12.85±0.64 12.4-13.3 2	—	1
Interorbital breadth	4.18±0.22 3.9-4.4 4	4.23±0.10 4.1-4.3 4	4.05±0.10 4.0-4.2 4	4.25±0.13 4.1-4.4 4	4.10±0.14 4.0-4.2 2	4.3	4.2	4.25±0.07 4.2-4.3 2	—	2
Cranial breadth	11.40±0.36 11.1-11.9 4	11.95±0.37 11.6-12.4 4	11.38±0.26 11.0-11.6 4	12.07±0.21 11.9-12.3 3	12.0±0.00 — 2	11.8	11.9	12.0	—	—
Length of incisive foramina	5.58±0.26 5.2-5.8 4	5.78±0.30 5.4-6.1 4	5.82±0.26 5.5-6.2 5	6.05±0.31 5.6-6.3 4	6.05±0.07 6.0-6.1 2	5.4	5.9	5.15±0.35 4.9-5.4 2	—	1
Length of bony palate	3.98±0.33 3.5-4.2 4	4.10±0.18 3.9-4.0 4	3.96±0.15 3.8-4.2 5	4.00±0.00 — 4	4.10±0.14 4.0-4.2 2	4.1	4.2	3.55±0.07 3.5-3.6 2	—	2
Alveolar length of M ¹ -M ³	4.65±0.13 4.5-4.8 4	4.98±0.19 4.7-5.1 4	4.72±0.08 4.6-4.8 5	4.95±0.06 4.9-5.0 4	5.05±0.07 5.0-5.1 2	4.8	5.0	3.95±0.21 3.8-4.1 2	—	2

^a In molt from juvenile to subadult.

so far do not contain *lepturus*. The high, cold, and wet forests of Cerro San Felipe, which seem similar to habitat on the Sierra de Juárez (although may not be in terms of microhabitat), are occupied by *Peromyscus difficilis*, a mouse of about the same size as *lepturus* but not closely related to it. Certainly a careful ecological and distributional study of the species of *Peromyscus* that occupy the mountains of northern Oaxaca is needed.

Peromyscus lophurus

This species has been recorded from the highlands of Chiapas, Guatemala, and El Salvador. The Chiapan specimens I examined are from San Cristóbal in the Mesa Central (four U.S.N.M.), and from Pinabete (five U.S.N.M.) and Triunfo (six U.M.M.Z.) in the Sierra Madre de Chiapas. The Guatemalan material is from Distrito Huehuetenango, Todos Santos (six U.S.N.M.); Distrito Totonicapan, Cael, (two U.S.N.M.); and Distrito San Marcos, south slope of Volcán Tajumulco (one U.M.M.Z.). The example from El Salvador is from Distrito Chalatenango, Los Esesmiles (one M.V.Z.). I have not seen the two specimens from Ambos de Triunfo, Chiapas, that Villa R. (1949, p. 516) recorded as *lophurus*.

The known altitudinal range of *lophurus* is from 6400 feet (Triunfo, Chiapas) to 10,200 feet (Cael, Guatemala).

Judged from the meager information on habitat in published reports, *lophurus* is an inhabitant of cold and wet oak and conifer forests. According to Goldman (1951), he and E. W. Nelson worked in this type of forest around San Cristóbal, Pinabete, Cael, and Todos Santos. Triunfo is also in a cloud-forest belt (Hooper, 1947). The specimen from Los Esesmiles supplies the easternmost record of the species. It was taken on a north-facing slope at 8000 feet in "rain forest," according to information on the skin label. In describing that area of Los Esesmiles, Burt and Stirton (1961, p. 11) wrote: "The north slope and summit are humid, dripping wet throughout the year. Here are large oaks covered with epiphytes and with an understory of tree ferns, shrubs, small ferns, and moss. It is a cloud forest." *Peromyscus oaxacensis* and *P. mexicanus* were taken in the same forest.

There seems to be no significant geographic variation in morphology of skins and skulls of available samples (measurements are listed in table 2). In addition to Osgood's (1909, p. 192) observations on variation in color of the tail, I detect some variation in tone of the pelage. Specimens from San Cristóbal, Todos Santos, and Cael are slightly brighter than those in comparable pelage from Triunfo, Pinabete, and

Volcán Tajumulco. Nevertheless, available samples are still too small for the full extent of individual, seasonal, and geographic variation in *lophurus* to be assessed.

Peromyscus simulatus

This species is still known only from the holotype and a paratype collected by E. W. Nelson and E. A. Goldman in July, 1893 (Osgood, 1909, p. 193). They obtained both specimens above Xico (Veracruz) on the steep Gulf slopes of the Cofre de Perote at about 6000 feet elevation. The meager information on their habitat comes from Goldman's (1951, p. 272) description of the forest on the Cofre at that elevation: heavy rains were usual at that altitude; fog and mist shrouded the slopes during the periods between rains; the forest was dense, cold, and wet and composed mainly of large oaks with some fir at slightly higher elevations. *Peromyscus furvus* and *P. thomasi nelsoni*, two other species of deep-forest *Peromyscus*, were taken at the same elevation as *P. simulatus*.

Hall and Kelson (1959, p. 646), followed by Hall and Dalquest (1963, p. 308), provisionally referred three specimens of *Peromyscus* from Teocelo, Veracruz, to *P. simulatus*. Through the courtesy of Drs. E. Raymond Hall and J. Knox Jones, Jr., of the University of Kansas Museum of Natural History, I have been able to examine those specimens (K.U. Nos. 30481-30483). All three are examples of *P. aztecus*, not *simulatus*. Their morphological features fall well within the range of variation seen in series of *aztecus* (in the University of Michigan Museum of Zoology) from Hidalgo, Puebla, and Veracruz.

SUMMARY

Based on data from skins, skulls, and genitalia, samples of *Peromyscus* from southern Oaxaca, described by Osgood as *angelensis* and regarded as a subspecies of *P. banderanus*, are placed in *P. mexicanus* rather than in *banderanus*. Examples of both species have been taken at the same place in southeastern Guerrero. Series of *Peromyscus* from Guatemala and Honduras originally recorded in the literature as *P. mexicanus saxatilis*, *P. guatemalensis tropicalis*, and *P. hondurensis* are reallocated either to *P. m. saxatilis* or to *P. oaxacensis*. *Peromyscus hondurensis* is a synonym of *oaxacensis*. These new allocations amplify known geographic distributions of *P. m. saxatilis* and *P. oaxacensis*. Information on taxonomy, geographic distribution, and habitat is summarized for *P. lepturus*, *P. lophurus*, and *P. simulatus*. *Peromyscus ixtlani*, based on samples from the mountains of northern Oaxaca, is considered a subspecies of *P. lepturus*. Specimens

allocated in the recent literature to *P. simulatus* are examples of *P. aztecus*; *simulatus* is still known only from the holotype and a paratype.

LITERATURE CITED

ANDERSON, SYDNEY

1968. A new craniometer and suggestions for craniometry. *Jour. Mammal.*, vol. 49, pp. 221-228, figs. 1-3.

BURT, WILLIAM HENRY, AND RUBEN A. STIRTON

1961. The mammals of El Salvador. *Misc. Publ. Mus. Zool. Univ. Michigan*, no. 117, pp. 1-69, figs. 1-2.

GOLDMAN, EDWARD ALPHONSO

1951. Biological investigations in México. *Smithsonian Misc. Coll.*, vol. 115, pp. 1-476, pls. 1-71.

GOODWIN, GEORGE G.

1932. Three new *Reithrodontomys* and two new *Peromyscus* from Guatemala. *Amer. Mus. Novitates*, no. 560, pp. 1-5.

1934. Mammals collected by A. W. Anthony in Guatemala 1924-1928. *Bull. Amer. Mus. Nat. Hist.*, vol. 68, pp. 1-60, pls. 1-5.

1941. A new *Peromyscus* from western Honduras. *Amer. Mus. Novitates*, no. 1121, p. 1.

1942. Mammals of Honduras. *Bull. Amer. Mus. Nat. Hist.*, vol. 79, pp. 107-195.

1955. Two new white-footed mice from Oaxaca, Mexico. *Amer. Mus. Novitates*, no. 1732, pp. 1-5.

1956. Seven new mammals from México. *Ibid.*, no. 1791, pp. 1-10.

1964. A new species and a new subspecies of *Peromyscus* from Oaxaca, Mexico. *Ibid.*, no. 2183, pp. 1-8, figs. 1-4.

- [In press.] Mammals from the State of Oaxaca, Mexico, in the American Museum of Natural History, *Bull. Amer. Mus. Nat. Hist.*, vol. 141, art. 1.

HALL, E. RAYMOND, AND WALTER W. DALQUEST

1963. The mammals of Veracruz. *Univ. Kansas Publ. Mus. Nat. Hist.*, vol. 14, no. 14, pp. 165-362, figs. 1-2.

HALL, E. RAYMOND, AND KEITH R. KELSON

1959. The mammals of North America. New York, The Ronald Press, vol. 2, pp. i-viii, 547-1083, figs. 313-552.

HOFFMEISTER, DONALD F.

1951. A taxonomic and evolutionary study of the piñon mouse, *Peromyscus truei*. *Illinois Biol. Monogr.*, vol. 21, no. 4, pp. 1-92, figs. 1-24, pls. 1-5.

HOOPER, EMMET T.

1947. Notes on Mexican mammals. *Jour. Mammal.*, vol. 28, no. 1, pp. 40-57.

1957. Dental patterns in mice of the genus *Peromyscus*. *Misc. Publ. Mus. Zool. Univ. Michigan*, no. 99, pp. 1-59, figs. 1-24.

1958. The male phallus in mice of the genus *Peromyscus*. *Ibid.*, no. 105, pp. 1-24, 1 fig., pls. 1-14.

1961. Notes on mammals from western and southern Mexico. *Jour.*

- Mammal., vol. 42, no. 1, pp. 120-122.
- [In press.] Classification. In King, John A. (ed.), *Biology of Peromyscus*. Amer. Soc. Mammal., Spec. Publ., no. 2.
- HOOPER, EMMET T., AND GUY G. MUSSEY
1964. Notes on classification of the rodent genus *Peromyscus*. Occas. Papers Mus. Zool. Univ. Michigan, no. 635, pp. 1-13, figs. 1-2.
- MERRIAM, C. HART
1898. Descriptions of twenty new species and a new subgenus of *Peromyscus* from Mexico and Guatemala. Proc. Biol. Soc. Washington, vol. 12, pp. 115-125, 1 fig.
- MUSSEY, GUY G.
1964. Notes on geographic distribution, habitat, and taxonomy of some Mexican mammals. Occas. Papers Mus. Zool. Univ. Michigan, no. 636, pp. 1-33, 1 fig.
1968. A systematic study of the Mexican and Guatemalan gray squirrel, *Sciurus aureogaster* F. Cuvier (Rodentia: Sciuridae). Misc. Publ. Mus. Zool. Univ. Michigan, no. 137, pp. 1-112.
- OSGOOD, WILFRED H.
1904. Thirty new mice of the genus *Peromyscus* from Mexico and Guatemala. Proc. Biol. Soc. Washington, vol. 17, pp. 55-77.
1909. Revision of the mice of the American genus *Peromyscus*. North Amer. Fauna, no. 28, pp. 1-285, figs. 1-12, pls. 1-8.
- VILLA, R., BERNARDO
1949. Mamíferos del Soconusco, Chiapas. Anal. Inst. Biol., Mexico, vol. 19, pp. 485-528, 1 map.

